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THE USAGE OF THE DIGITS OF A CAPTIVE AYE-AYE (*Daubentonia madagascariensis*)

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ABSTRACT A study was carried out between July and August 1989 on the usage of the manual digits of one captive aye-aye (*Daubentonia madagascariensis*) at the Tsimbazaza Zoo, Antananarivo. Manipulation of the digits was examined by direct observation and by analysis of tapes taken with a video-camera.

The third digit (the most slender) and the fourth digit (the longest) of both hands, were used for scooping foods: the average duration of one scoop was 11.9 seconds for the third digit and 14.7 seconds for the fourth digit, with no substantial difference between them (t-test, $p > 0.05$). The aye-aye alternated between using the third and fourth digits, according to the foods presented.

The third digit was also used for tapping food. The average duration of one tapping bout was 2.9 seconds. The fourth digit was often used for grooming and for grasping a twig or holding onto wire mesh while traversing.

This report forms the experimental part of a series of papers examining the hard-nut adaptation hypothesis of the aye-aye's ecological niche. In this investigation, the captive female aye-aye showed some extraordinary examples of feeding behavior. The aye-aye ate all foods except sugar cane, by using her third and fourth digits after tapping the food with her third digits. Primates often feed by holding a food item with the hands and biting off pieces directly with the mouth. But the aye-aye did not eat in such a manner. This feeding behavior shows the specialization for consuming the contents of hard nuts of ramy (*Canarium* spp.) under natural conditions, and that the aye-aye's morphological characteristics are closely adapted to such a feeding method.

KEY WORDS: Aye-aye; *Daubentonia madagascariensis*; Scooping; Tapping; Hard-nut adaptation hypothesis.

INTRODUCTION

The characteristic morphological features of the aye-aye and, especially, the singular form of its fingers have attracted the attention of researchers since its discovery. In particular, the way the fingers are used during feeding has been the focus of a number of observations (Sonnerat, 1782; Owen, 1863; Petter, 1977; Petter et al., 1977). These studies, however, were for the most part fragmentary and confined to the usage, during feeding, of the third digit, the most slender of all the digits. Nevertheless, food-tapping behavior with the third digit has not been reconfirmed since the first description by earlier researchers (Petter, 1977). In short, it can be said that no reliable observation has been made on the usage of the fingers of the aye-aye.

In comparison with other primates, the aye-aye has several quite specialized mor-

phological traits: the large continuously growing incisors (right and left incisors which can be moved independently from each other); rodent-like dentition (I:1; C:0; P:0; M:3 for upper, and I:1; C:0; P:1; M:3 for lower); large, movable, membranous ears; claws at the tips of all digits except the great toes; extremely slender third manual digits and then special structure, and nipples around the inguinal region (Owen, 1863; Petter, 1977; Tattersall, 1982).

The relationship between the aye-aye's specialized morphological traits and its survival tactics and feeding habits, and the possibility that these features work together to help the aye-aye exist, are questions that first come to the mind when observing an aye-aye, because the aye-aye is far removed in its morphology from other primates.

In answer to the above questions, all that I have acquired from previous observations is that the aye-aye extracts the edible parts of hard nuts or the insides of branches using the third digits and incisors.

The same situation exists regarding the studies on the movable, membranous ears of the aye-aye. The reported observations indicate that they are used for searching insect larvae hidden within branches (Petter, 1977). If my hypothesis that the staple food of the aye-aye is the hard-shelled ramy nut is valid (Iwano & Iwakawa, 1988), new insights into the function of the aye-aye's ears shall be gained.

A study has been ongoing from June 1989 on the nocturnal activity of the aye-aye housed in the Botanical and Zoological Park of Tsimbazaza, Antananarivo. This study was undertaken to elucidate the nocturnal activity of the aye-aye, including the usage of the digits, and the results reported here were obtained between July and August 1989.

METHODS

The adult female aye-aye observed in this study was brought to the Botanical and Zoological Park of Tsimbazaza around September 1988. The animal was reported to have been captured near Antsohihy along the north-west coast of Madagascar, but the details of capture remain unclear.

The aye-aye was housed in a two-part enclosure: a feeding room 2.5 m wide, 2.15 m long and 2.5 m high, and a cage 3.8 m wide, 3.8 m long and 2.5 m high. The two rooms were separated by a concrete wall with a small window through which the two rooms were connected. The side walls and ceiling of the cage, and the rear surface of the feeding room were covered with wire mesh. The front part of the feeding room was fitted with a glass panel. Because the aye-aye ate foods in a dish placed on the floor of the feeding room, I could observe its usage of the digits from a very close distance through the glass window.

Period of observation spanned 13 nights between June 7 and August 30, 1989, and the total direct observation time was 133 hours. The total number of observation units was 15,678 (one observation continuum of 30 seconds duration was taken as one unit), and the usage of digits was confirmed to account for about 3% (429 units).

Observations were made for 11 hours from 18:00 to 5:00 the next day and recorded, following an instantaneous sampling method with a 30 second duration (Altmann, 1974). Notes were made as to which fingers of each hand were used for feeding and grooming, and the names of foods eaten.

Because the aye-aye was active only in the dark, it was difficult to precisely observe the details of its behavior even in captivity. In addition, the aye-aye used its digits so fast that their movements often escaped observation by the naked eye. To supplement visual observation, a video-camera was introduced.

The video-camera was kept running, over five nights, on July 22 and 23 and August 15-17, with the filming time totaling 109 minutes. Two sets of illumination lamps (each of 150,000 lux) were used continuously. Despite the light, the aye-aye ate facing the light and did not deliberately avoid it.

The aye-aye was presented with the following foods: coconuts, ramy fruits (*Canarium madagascariense*), papayas, passion fruits, bananas, tomatoes, sugar cane, rice, raw eggs, honey, coconut milk, and bread (coated with honey or soaked with condensed milk). Observation on feeding were made using these food items, except the last three. In addition, an artificial food item was prepared by stuffing sugar cane into the cavity of a bamboo.

The aye-aye was given five to seven food items at about 16:00 and thereafter, the feeding room was left undisturbed. When taking videos, however, the feeding method was modified: after the aye-aye was confirmed to be active, a food item was given, and it was exchanged for another only when the animal no longer showed interest in it.

RESULTS

I. Storage and Preference of Food Items

When the aye-aye was given a whole coconut (July 22), a considerable time (i.e. 93 min.) passed before it could eat it. Probably because the animal became impatient with such a long and tedious preparatory work, the aye-aye three times retrieved pieces of coconut from under the nest box where it had hidden them the day before. Whenever I noticed the aye-aye to do so, I entered the feeding room to search for other hidden coconut fragments to remove them. Despite such efforts, the animal was frequently observed to retrieve coconut fragments which were hidden somewhere.

After the aye-aye fed on a coconut, I replaced it with eggs. After half an hour, I gave the animal a second egg, which it did not eat, retrieving, instead, a piece of coconut hidden in the back of the nest box.

Prior to feeding the next day, the keeper searched for hidden coconut fragments and removed them. The aye-aye, however, again retrieved pieces of coconut from somewhere. Thus, from then on it was always necessary to search for hidden coconuts before videotaping the aye-aye's feeding activity. Such food storing habits of the aye-aye have not been reported before.

The aye-aye showed a definite preference toward some test food items. Ramy

fruits were consumed most quickly, followed by coconuts and sugar cane. The aye-aye ate bananas, eggs, tomatoes, papayas, rice, passion fruits and bread coated with honey or soaked with milk, but did not eat oranges.

When presented with the artificial food item made with a piece of bamboo stuffed with sugar cane, the aye-aye first sniffed it, then tapped it with the third digit, split it by biting, scooped out the sugar cane packed within, using the third and fourth digits, and ate it.

II. Direct Observation on the Usage of Digits

Direct identification of digits was difficult due to the darkness in the feeding room, and the digits were often concealed under the movements of the hands and body. Furthermore, the digits moved quickly. Thus, the proportion of movements escaping my attention would be considerable.

1. Usage of Digits Classified by Types of Activities (Table 1)

A total of 429 observation units were recorded, of which 59% (254 units) comprised the usage of the third digits.

Usage of the third digits can be classified into three categories: scooping food, grooming and tapping. The fourth digits were used for scooping and grooming. The fourth digits were also used for grasping branches during movement or hanging on the wire mesh, but such activities were excluded from the present study.

Both the third and fourth digits were used frequently for feeding (67.7% and 86.8%, respectively). When feeding, the third digit on the left hand and the fourth digit on the right hand were more frequently used. This tendency, however, appeared to be an artifact of sampling and my impression was that the animal used both hands with no inclination toward laterality.

Few observation units were recorded during which the third digits were used for grooming, and how they were used was, thus, unclear.

Tapping of food was done solely by the third digits. The aye-aye taps on various objects such as foods, the surface of trees, the ceiling of the nest box, etc. However, percussion movements were so fast that they often escaped my detection.

2. Usage of Digits Classified by Food Items (Table 2)

A total of 324 observation units during which usage of digits was confirmed for

Table 1. Comparison of the usage of the third and fourth digits for various activities measured by the instantaneous sampling method between July 9 and August 30, 1989.

	Third digit			Fourth digit			Total
	Right	Left	Total	Right	Left	Total	
	unit (%)	unit (%)	unit (%)	unit (%)	unit (%)	unit (%)	
Feeding	53 (51.5)	119 (78.8)	172 (67.7)	93 (90.3)	59 (81.9)	152 (86.3)	324
Grooming	18 (17.5)	10 (6.6)	28 (11.0)	10 (9.7)	13 (18.0)	23 (13.1)	51
Tapping	32 (31.1)	22 (14.6)	54 (21.3)	—	—	—	54
Total	103	151	254	103	72	175	429

One unit is 30 seconds duration.

Table 2. Comparison of the usage of the third and fourth digits for feeding on various food items measured by the instantaneous sampling method between July 9 and August 30, 1989.

	Banana	Tomato	Papaya	Coconut	Ramy	Egg	Bread	Others	Total
Digit									
3rd Right	11 (36.7)	1 —	4 —	12 —	17 (34.0)	7 (17.5)	1 —	0 —	53 (30.8)
Left	19 (63.3)	6 —	11 —	10 —	33 (66.0)	33 (82.5)	1 —	6 —	119 (69.2)
Total	30	7	15	22	50	40	2	6	172
4th Right	71 (59.2)	21 (67.7)	1 —	0 —	0 —	0 —	0 —	0 —	93 (61.2)
Left	49 (40.8)	10 (32.3)	0 —	0 —	0 —	0 —	0 —	0 —	59 (38.8)
Total	120	31	1	0	0	0	0	0	152

One unit is 30 seconds in duration. Values in parentheses are percentages of total units.

feeding were recorded. Usage of the third digits accounted for 53% (172), indicating nearly equal usage of the fourth digits.

Usage of the third and fourth digits changed discriminatory according to the food item eaten: the fourth digits were preferentially used for bananas and tomatoes (about 80%), the third digits were exclusively used for coconuts, ramy fruits and eggs, and for papayas, the third digits were used nearly exclusively, except in one case.

III. Analysis of VTR Records of the Usage of Digits during Feeding

A total 109 minutes of video tape were recorded. The usage of the digits was confirmed to include 334 seconds (117 occasions) for tapping, 1,178 seconds (99 occasions) for scooping with the third digits, and 679 seconds (46 occasions) for scooping with the fourth digits. Judging from the video images, the following seven food items were confirmed to be consumed by the aye-aye: coconuts, ramy fruits, bananas, rice, passion fruits, sugar canes and eggs. The aye-aye altered its use of digits depending on the food item.

1. Feeding Process Classified by Food Items

(1). Coconuts (Fig. 1)

In general, coconuts were presented in 5 to 10 cm pieces. The aye-aye typically held a piece of coconut with both hands, gnawing the pulp with the lower incisors. The two lower incisors of the aye-aye are longer than other teeth, and therefore, effective for scooping out the contents of food items.

Once, shooting the video tape, I gave the aye-aye a whole coconut, so it had to first open the shell by gnawing. The usage of the digits was selective, depending on the process. In the initial process (Process I), the aye-aye made a large opening on the shell. In the next process (Process II), the aye-aye ate the coconut. Process I consisted of smelling, gnawing and tapping with the third digits (Fig. 1, upper). By contrast, Process II included the typical feeding activities of eating the contents (embryo and albumen). The usage of third and fourth digits were appropriately selective, according to the individual steps: The fourth digit was used for breaking

the contents into large pieces while the third digit was used for carrying the pieces to the mouth.

(2). Ramy nuts (Fig. 2)

In the wild, the aye-aye initially scrapes off the pulp with the incisors and then ex-

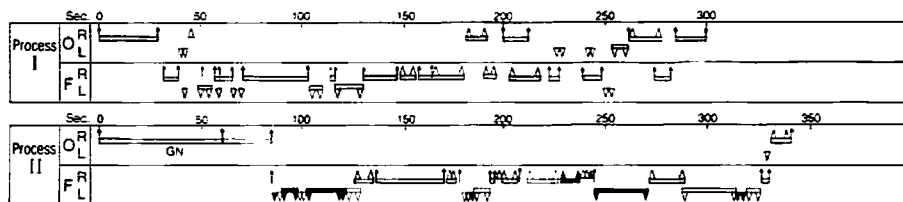


Fig. 1. Feeding process of the aye-aye on coconut (July 22, 1989).

I: First process started 19:47; II: Second process started 20:00.

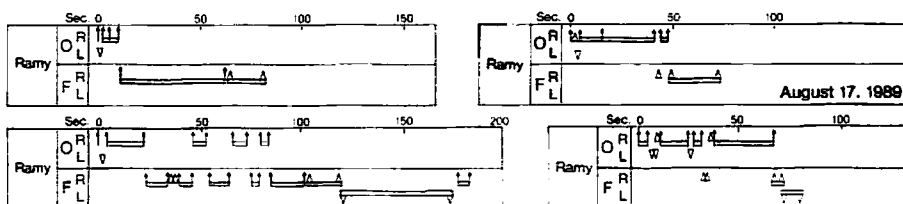


Fig. 2. Feeding process of the aye-aye on ramy nuts (August 17, 1989).

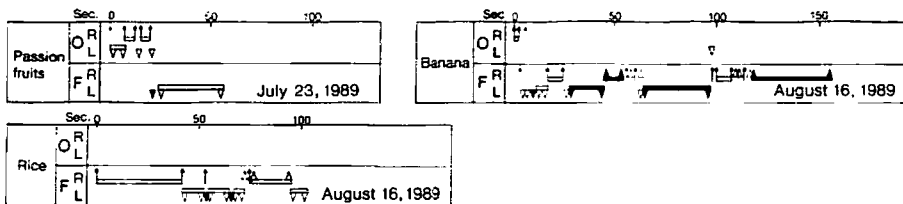


Fig. 3. Feeding process of the aye-aye on various foods (1).

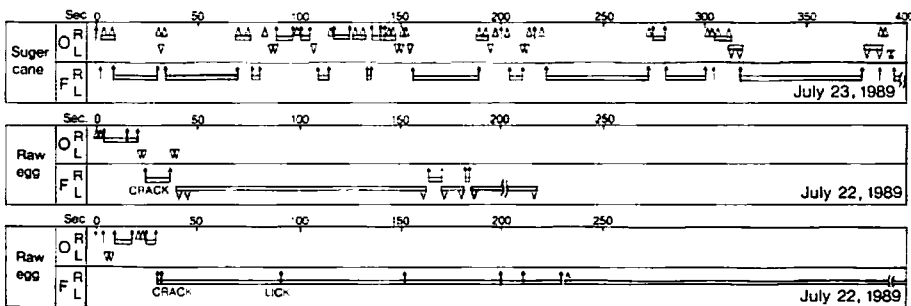


Fig. 4. Feeding process of the aye-aye on various foods (2).

O: Tapping etc. R: Right hand \triangle : 3rd digit \blacktriangle : 4th digit \triangle : 3rd or 4th digit (unidentified)
 F: Feeding L: Left hand ∇ : 3rd digit \blacktriangledown : 4th digit \uparrow : Gnaw, smell and lick
 =: Right hand —: Left hand

tracts the embryo within the nut using the third digits. The total feeding time required 102 seconds to consume one ramy nut on average (Iwano & Iwakawa, 1988). The aye-aye in captivity, on the other hand, sometimes ate the contents while engaged in widening a hole on the nut surface by gnawing, suggesting that there may be slight differences in feeding behavior between individuals in the wild and in captivity. Aside from such minor differences, however, the basic feeding process of the aye-aye in captivity did not vary much from that observed in the wild. The feeding time of the aye-aye in captivity on one ramy nut was 103 seconds on average (71–183 seconds, $N=4$).

(3). Passion fruits, rice and bananas (Fig. 3)

When given a passion fruit, the aye-aye smelled, tapped, bore a hole into the pulp by gnawing, broke through the hole by inserting the fourth digit, and extracted the contents using the third digit. The aye-aye, however, apparently did not favor passion fruits, because it refused to eat a second fruit after consuming the first one.

At first, the aye-aye ate rice with its mouth directly, but later switched to using the third and fourth digits to carry it to the mouth.

Of all the observation units during which feeding on bananas was confirmed, about 80% showed usage of the fourth digit. Analysis of the video images also demonstrated that about 91% of the time consumed for scooping up the content of bananas consisted of the usage of the fourth digit.

(4). Sugar cane and eggs (Fig. 4)

The aye-aye did not scoop with the digits for feeding on a sugar cane. While eating the sugar cane, the aye-aye frequently tapped the cane stem with the third digit during intervals between biting the pulp and sucking the juice, as if searching for a location more vulnerable to a bite.

The aye-aye bit and made a small opening on an egg-shell through which it extracted the content by scooping it out with the third digit. The third digit was used continuously for eating eggs (maximum of 178 seconds).

2. Continuous Use of Digits

The average time span during which the third digit was continuously used for tapping remained the same regardless of whether it happened to the right or left hand (2.9 seconds for the left and 2.8 seconds for the right).

When feeding on ramy nuts, the aye-aye initially ate only after smelling it without engaging in tapping or other preparatory inspections which are commonly performed for other food items. This behavior suggests its familiarity with this particular food item. It is noteworthy that the aye-aye, when given an unripened ramy fruit, simply sniffed and refused it without any tapping.

In general, the average time span for scooping with the third digits (11.9 seconds) showed no substantial difference from that for the fourth digits (14.7 seconds; t -test, $p>0.05$). When feeding on bananas, the fourth digits were preferentially used regardless of laterality. The third digits (both right and left) were used for scooping for a span of 3 seconds on average while the fourth digits were used for 13.7 seconds on average for the right and 32.8 seconds for the left.

The average time spent scooping was greatest when feeding on eggs (47.1

seconds, $N=8$), equivalent to five times the average time span (9.2 seconds) for other food items. Also noteworthy in feeding on eggs is that the aye-aye did not exchange hands during scooping.

The average time spans for scooping during feeding on coconuts and ramy fruits were 8.4 seconds ($N=52$) and 11.8 seconds ($N=10$), respectively. The difference in two values was not significant (t -test, $p>0.05$).

The average time span for scooping with the fourth digits was slightly longer for bananas (21.2 seconds, $N=10$) than for coconuts (14.4 seconds, $N=28$; t -test, $p<0.05$).

DISCUSSION

The aye-aye puts its digit into the food items and scoops up food. The aye-aye uses both the third and fourth digits for this purpose, but the third digits seem to be more adapted for this activity because they are very slender, and less than half the width of the fourth digit.

The singular feeding behavior of the aye-aye of eating food with its fingers has long attracted attention, but solid observational data is still lacking. Sonnerat (1782, quoted in Owen, 1863) reported, "the animal makes use of the middle digit to draw out of holes in trees the worms which form its food." This early investigator contended that the third digit was used for feeding on insect larvae.

Sandwith (in a letter quoted in Owen, 1863) reported that the aye-aye tapped with the third digit on the bark of a branch possibly hiding insect larvae, inserted the digit into a hole, bit away the bark, and took out the larvae to eat. He added further that the third digit was also used for drinking water.

Substantial additions to those early observations, immediately after the discovery of the aye-aye, have been made by later researchers, who clearly noted that the aye-aye fed in the wild on insect larvae, coconuts, litchis, mangoes and the sap of *Hintsyna* (*Afzelia bijuga*). Further, in captivity, the aye-aye ate bananas, raw eggs, rice boiled in soup, sugar cane and honey. These observers further identified the exclusive use of the third digits for eating coconuts, insect larvae and eggs, and combined use of the fourth digits for eating bananas (Petter & Peyrieras, 1970; Petter, 1977; Petter et al., 1977). They did not, however, confirm usage of the third digit for tapping on food ("We have never observed, however, the third finger used as a percussion instrument, as has been described by early observers.": Petter, 1977).

Recently, aye-ayes have been directly observed in the Nosy Mangabe Special Reserve. The bark of *Hintsyna* (*Afzelia bijuga*) and bamboos (*Bambusa vulgaris*, Pollock et al., 1985), and nuts of ramy (*Canarium madagascariense*, Iwano & Iwakawa, 1988) were newly added to the diet of the aye-aye in the wild. Although the third digit was found to be used for eating ramy nuts, it was never observed to be used for tapping on food.

Examination of the skeleton (Parc Tsimbazaza, No. 1262) of a young adult male aye-aye stored in the specimens room of the Botanical and Zoological Park of Tsimbazaza (Table 3) showed that the metacarpal is continuous with the third digit

Table 3. Size of the aye-aye's manual digits (Sample No. 1262, Parc Tsimbazaza).

	Claw		Second		Third		Metacarpus		Total length
	L	W	L	W	L	W	L	W	
<i>Right hand</i>									
Pollex	16.9	3.9	21.2	6.8	—	—	—	—	38.1
Index	16.5	2.6	20.2	3.9	31.0	3.9	—	—	67.7
Medius	7.6	1.4	17.6	1.9	41.9	2.7	17.7	4.3	84.8
Annularis	16.7	3.2	37.2	4.3	49.1	5.1	—	—	103.0
Minimus	15.9	3.8	24.0	4.4	33.5	4.2	—	—	73.4
<i>Left hand</i>									
Pollex	18.3	—	20.9	5.9	—	—	—	—	39.2
Index	17.0	2.7	20.3	3.7	31.2	4.2	—	—	68.5
Medius	7.8	1.3	18.8	1.9	42.7	2.6	17.8	3.7	87.1
Annularis	16.5	3.2	37.3	4.7	52.4	5.2	—	—	106.2
Minimus	16.8	3.0	24.3	4.2	34.8	4.3	—	—	75.9

L: length; W: width (unit: mm).

and protrudes about 18 mm from the palm. Furthermore, the joint with the phalanx is so firmly fixed that the third digit cannot grasp nor hang from a branch as can the fourth digit. The third digits appear to be specially adapted for scooping during feeding, grooming and tapping. When using the third digit for tapping, the aye-aye slants its large, membranous ears forward, apparently to listen to the sound generated by percussion (Plate 1), suggesting a close relationship between the two specialized structures of the digit and ears.

I assume that the aye-aye's ears detect the thickness of the shell of a nut or the nature of its contents (insect larvae also are one of the contents) by analyzing the sound reflected from the object. I find it unlikely that its ears are for catching the sounds generated by insect larvae crawling within a branch.

It should be added that when the aye-aye gnaws on a hard object, muscular tension upon its face is increased, which sometimes results in forward and downward

**Plate 1.** The aye-aye used the third digits for tapping on the surface of sugar cane.



Plate 2. The aye-aye sometimes used the third digits to feed on tomatoes.

movement of the ears.

During feeding, the joint of the third digit can either be bent ventrally or dorsally (Plate 2). During this sequence, the third digit moved flexibly and smoothly as if it had no bone in its interior. The third digit appears to be markedly different in structure from other digits, but this question cannot be solved without more detailed study.

The aye-aye alternates its usage of the third and fourth digits according to food items, which may be principally related with the structure of the fourth digit. The fleshy part beneath the claw of the fourth digit does not widen as do other digits, excluding the third digit (compare the second and fourth digits holding the tomato in Plate 3). This fact suggests that the fourth digit is always used in association with feeding.

The claw of the fourth digit is more than two times longer and wider than that of the third digit, and as a whole, the fourth digit is stouter than the third digit. When feeding on passion fruits, the aye-aye, after peeling off the pulp with the incisors, used the fourth digit. This can be explained by assuming either that the hard shell can not be broken open by the third digit or that operations requiring more skill and force are allotted to the fourth digit. This assumption was apparently corroborated by observations of the aye-aye feeding on coconuts. The aye-aye, immediately after making a large opening in the shell with its incisors, extracted the contents while simultaneously breaking it into pieces with the fourth digit, thereby



Plate 3. The aye-aye ordinarily used the fourth digits to feed on tomatoes (81.6%).

making it easier to use the third digit for feeding. The fourth digit was mainly used for eating bananas and tomatoes. This is probably because the fourth digit can scrape out a greater quantity in one stroke than the third digit.

Why does the aye-aye use the digits to feed on such food items as bananas, tomatoes, papayas, and uncooked rice and eggs? This may be explained by the feeding behavior of the aye-aye in the wild. It has been demonstrated (Iwano, 1991) that ramy nuts (*Canarium* spp.) constitute the staple food of the aye-aye, as postulated by Iwano & Iwakawa (1988). Feeding on those fruits would be impossible without using the third digit. This also holds true for another important food item of the aye-aye, the wood-boring insect larvae. Because the larvae preferentially inhabit dead trees, scooping the larvae out with a slender digit represents a quite effective feeding method. It is possible that the aye-aye is so well adapted to such feeding methods that it also applies the same method to novel food items.

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